

30. On the Feet and Glands and other External Characters of the Paradoxurine Genera *Paradoxurus*, *Arctictis*, *Arctogalidia*, and *Nandinia*. By R. I. POCKOCK, F.R.S., F.L.S., F.Z.S., Curator of Mammals.

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This paper, the result of researches carried on at intervals for several years in the Society's Prosectorial Department, may be regarded as a continuation of the one dealing with the genera of Viverrinæ which was published in the 'Proceedings' for March 1915 (pp. 131-149). Its subject-matter is treated on the same general lines as those therein adopted, and its main purpose is to show first that the genera discussed, hitherto diagnosed mainly by cranial and dental characters, may be equally well, perhaps better, distinguished by the cutaneous features examined; and secondly, that these features fully justify the conclusion, hinted at but not adopted by Mivart, that the Viverrine and Paradoxurine genera should be relegated to distinct subfamilies of the Viverridæ.

The genus *Paradoxurus*, including the species referred to *Paguma* and *Macrogalidia*, ranges from India and Ceylon to the Philippine Islands and Celebes. *Arctictis* extends from the eastern Himalayas to Borneo, and *Arctogalidia*, with the same eastern limit, reaches Assam. *Nandinia*, on the contrary, is restricted to the forests of tropical Africa.

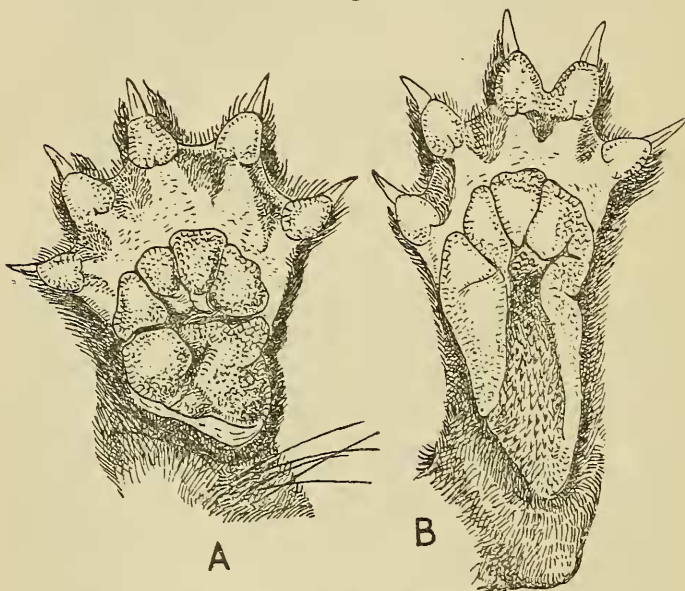
The Feet of Paradoxurus.

Of this genus I have examined examples of the three species *P. larvatus* from Szechuen, *P. niger* from India, and *P. hermaphroditus* from Singapore. According to Gray's nomenclature, which there is a tendency at the present time to revive, *larvatus* should be referred to the genus *Paguma*; but in this paper I propose,

without prejudice, to follow Blanford and most modern authors in regarding *Paguma* as a synonym of *Paradoxurus*.

The fore foot of *P. larvatus* is broad; the digits are capable of considerable distension and are webbed up to the proximal ends of the digital pads; the underside of the webs is smooth, save for the presence of four patches of short hair near the distal margin of each. The pollex is well developed and lies close to the second digit. The plantar pad is large and wide owing to the size of its pollical lobe, which approximately equals in dimensions any one of the three main lobes corresponding to the intervals between the

Text-figure 1.



Paradoxurus larvatus.

A. Left fore foot, digits fully stretched.

B. Left hind foot, " "

four principal digits. The lobes are well defined by grooves. The double carpal pad, separated by a deep naked crease from the plantar pad, is at least as wide and long as the latter including its pollical lobe. The external lobe of the carpal pad is about twice as large as the internal and is defined from it by a deep groove. These carpal pads occupy practically the whole width of the paw behind the plantar pad and, like the latter and the digital pads, are covered with coarsely granular or scale-like integument.

The claws are protected by rudimentary skin-lobes and are

retractile in the sense that the terminal phalanx can be drawn back so as to lie along the outer side of the penultimate phalanx as in most of the Viverridæ and the Felidæ.

The hind foot resembles the fore foot in its main features, but is narrower and the digital pads of the third and fourth digits are united at the base; behind their point of junction there is a small triangular patch of short hair. Similar patches of hair are present on the underside of the proximal half of the webs, as in the fore foot. The hallux is shorter than the pollex, but the hallucal lobe is large and adds considerably to the width of the plantar pad, the elements of which are well defined. Behind the plantar pad the greater part of the underside of the metatarsus is naked; the naked area, narrowing posteriorly or proximally, reaches to within about half an inch of the heel, which is covered with hair. This naked area exhibits a median depression which is narrower distally close to the plantar pad than proximally towards the heel, and is bounded at the sides nearly throughout its length by two thick ridges of integument, the metatarsal pads. The external of these, narrower but a little longer than the internal, is continuous distally with the external lateral lobe of the plantar pad; the internal is similarly continuous with the hallucal lobe of that pad. In the specimen here described, the depression between these pads or ridges is thickly covered with horny sub-spiniform papillæ.

The feet of *Paradoxurus hermaphroditus* and *P. niger* show no differences of moment from those of *P. larvatus*. The underside of the webs, however, is naked; and the example of *P. niger* examined exhibited no sharp horny papillæ in the depression between the metatarsal pads of the hind foot.

The Feet of Arctictis.

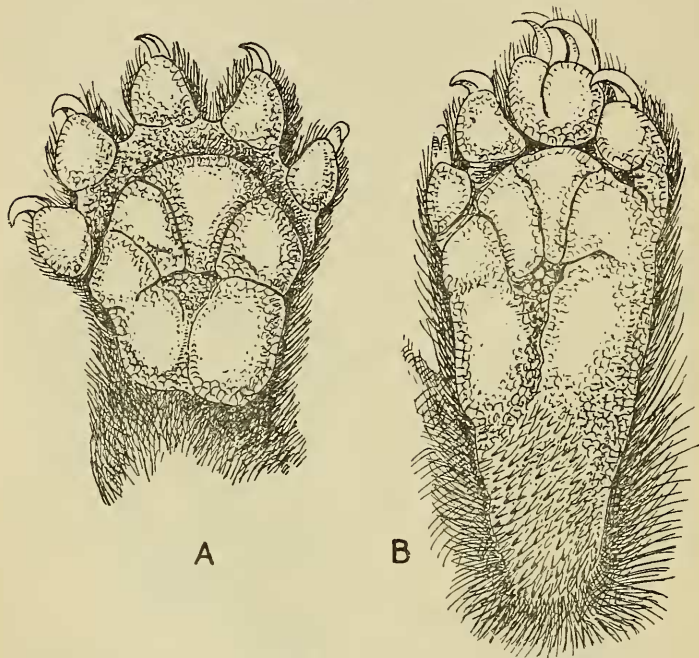
The fore foot resembles in all essential respects that of *Paradoxurus larvatus*, but the web connecting the digits is naked beneath, and the two elements of the carpal pad are not so sharply defined from one another and from the plantar pad.

The hind foot is also like that of *Paradoxurus* in most respects, particularly, be it noted, in the fusion of the digital pads of the third and fourth digits proximally. Here also there is no hair on the underside of the interdigital webs, the division between the plantar and metatarsal pads is ill-defined, and the metatarsal area itself is not sharply differentiated into a median depression and lateral elongated pads. On the contrary, it is comparatively flat and the naked area extends right back to the heel. In one example, a full-sized but young male, the skin of the underside of the heel is covered with a mat of horny, pointed papillæ. No such mat, however, is present on the heel of a young female, and, judging from the skins in the British Museum, its development is variable, the sculpturing being sometimes papillate, sometimes squamous.

The claws are sharp, strongly curved, and retractile, but are unguarded by lobes of skin.

In the nakedness of the heel, *Arctictis*, as has been noticed by Mivart and others, differs from all other genera of *Paradoxurines*.

Text-figure 2.



Arctictis binturong.

A. Left fore foot, digits partially stretched.

B. Left hind foot, digits not stretched.

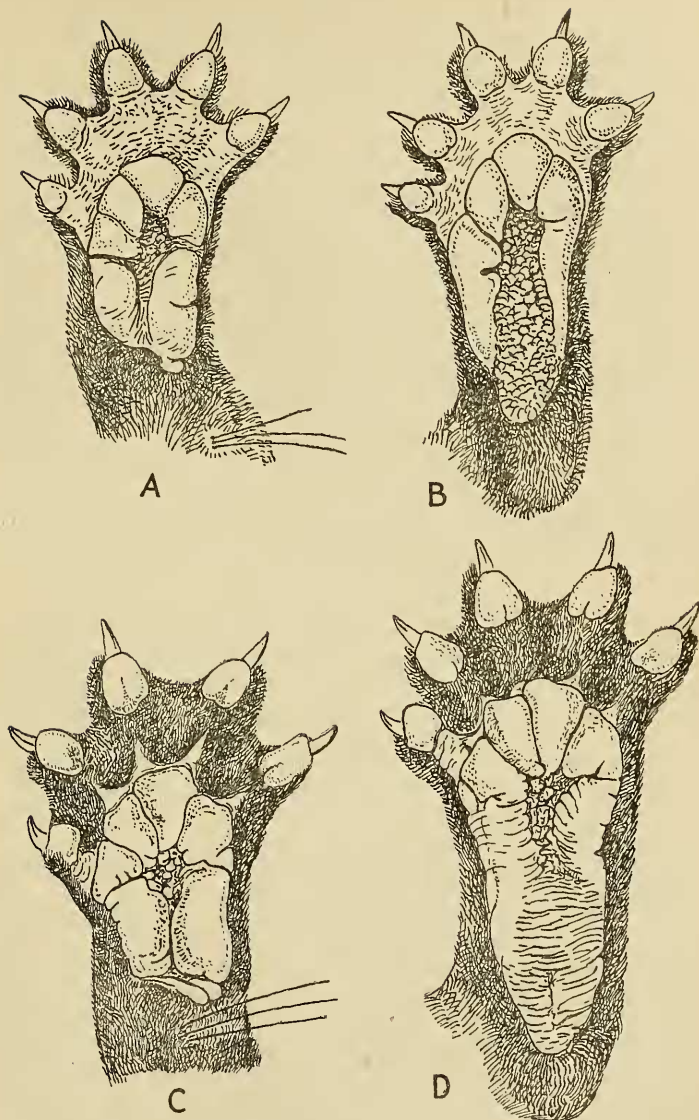
This may be an adaptation to a more thoroughly arboreal life—a conclusion supported by the prehensile power of the tail*; but I cannot find any record of the proximal fusion of the pads of the third and fourth digits. This character is very suggestive of affinity between *Arctictis* and *Paradoxurus*.

The Feet of Arctogalidia.

The feet of an example from Sarawak resemble in a general way those of *Paradoxurus*, but differ in one or two interesting particulars, especially in being longer, narrower, and less fully webbed. In the fore paw the digital and plantar pads are well

* About half an inch of the end of the tail was naked and formed a conical point to that organ calculated to enhance its grasping capacity.

Text-figure 3.



Aretogalidia, from Sarawak.

- A. Left fore foot, digits fully stretched.
 B. Left hind foot, " "

Nandinia binotata.

- C. Left fore foot, digits fully stretched.
 D. Left hind foot, " "

developed in the matter of thickness, but are covered with smooth integument, and the four lobes of the plantar pad are separated by shallow grooves and are therefore somewhat ill-defined. The area between the digital and plantar pads is quite hairless and the edge of the webbing between the 1st and 2nd, 2nd and 3rd, and 4th and 5th digits, and to a less degree that between the 3rd and 4th digits, is more deeply emarginate than in *Paradoxurus*. The anterior and lateral borders of the plantar pad form a narrower curve than in that genus, the pollical lobe especially being set farther back with reference to the median lobe. The carpal pads are much longer and narrower, but are as wide throughout as the plantar pad. The claws are short and strongly curved and not protected by skin-lobes.

The hind foot differs from that of *Paradoxurus* in characters similar to those mentioned in connection with the fore foot, but one additional difference to be noticed is that the pads of the 3rd and 4th digits are not fused but are separated by a measurable extent of webbing. The naked area on the metatarsus is of about the same extent as in *Paradoxurus*, the heel being thickly hairy as in that genus; and in the skins examined the area between the two smooth lateral ridges, or metatarsal pads, is covered with coarsely squamous integument, the pads themselves, like the plantar and digital pads, being smooth as in the fore foot.

The Feet of Nandinia.

The feet of this genus have only been briefly described previously, so far as I have ascertained. Mivart (P. Z. S. 1882, p. 170) says that the tarsus and metatarsus are "about as bald as in *Paradoxurus*," which is true; but Lydekker's statement that the tarsus is partially bald as in *Hemigalus* is not in accord with the facts (Lloyd's Nat. Hist.: Cats etc., p. 228, 1896).

The fore foot resembles that of *Paradoxurus larvatus* in the development of the webs at least to the proximal ends of the digital pads, in the extent to which the toes are capable of separation, and in the confluence of the plantar and carpal pads to form a single mass, of which the component elements are defined merely by grooves. These pads, however, are longer as compared with their width than in *Paradoxurus*, and in the more backward position of the pollical lobe and the closer curvature of the distal margin of the plantar pad resemblance may be seen to *Arctogalidia*. A very narrow area of skin, sometimes giving off short streaks towards the digital pads of the 2nd, 3rd, 4th, and 5th digits, is naked, but otherwise the whole of the area between the plantar and digital pads is thickly covered with velvety hair as in *Genetta* and *Viverra*. In this respect the feet differ from those of *Paradoxurus**, *Arctictis*, and *Arctogalidia*. The underside of the pollex is, moreover, quite naked, the digital pad of this

* Hodgson, however, described this area in *Paradoxurus lanigerus* as hairy: but whether the hair was developed to the extent seen in *Nandinia* or in *Paradoxurus larvatus* does not appear.

digit, which is considerably shorter than in *Paradoxurus* and a little shorter than in *Arctogalidia*, being connected with the pollical lobe of the plantar pad by a bare strip of integument.

The claws are retractile but are not guarded by small skin-lobes as in *Genetta*. The pads are in the main quite smooth, but the central depression behind the plantar pad is somewhat coarsely sculptured.

The hind foot, so far as the webbing and the structure of the plantar pad are concerned, resembles and differs from that of the other genera described in this paper in the same respects as those mentioned in connection with the fore foot. The digital pads, however, of the third and fourth digits are widely separated, even more so than in *Arctogalidia*, and resemble in this respect the homologous pads of *Genetta* and other Viverrines. The whole of the posterior area of the naked metatarsal space is coarsely ridged transversely, and this ridging is replaced in the elongated depression behind the plantar pad by coarse polygonal sculpturing. This depression is bounded on each side by a thick, elongated, metatarsal pad, sculptured internally, but these pads are not so long as in *Paradoxurus* and *Arctogalidia**.

The characters of the feet of the four genera of Paradoxurines above described may be systematically epitomised as follows:—

- | | |
|--|----------------------|
| a. Pads of 3rd and 4th digits of hind foot proximally united in the middle line; fore paws broad, their plantar and carpal pads combined only a little longer than wide; pads of fore and hind feet with coarse tessellated sculpturing. | |
| a'. Sole of hind foot not naked to heel | <i>Paradoxurus.</i> |
| b'. Sole of hind foot naked to heel | <i>Arctictis.</i> |
| b. Pads of 3rd and 4th digits of hind foot separated; fore paws narrower, their plantar and carpal pads combined much longer than wide; pads of fore and hind feet smooth or nearly so; [heel of hind foot hairy as in <i>Paradoxurus</i>]. | |
| a ² . Area between plantar and digital pads smooth | <i>Arctogalidia.</i> |
| b ² . Area between plantar and digital pads, except of digit 1, thickly hairy | <i>Nandinia.</i> |

The tessellated sculpturing of the pads observed in *Arctictis* and the species of *Paradoxurus* examined must be verified for other species of the latter genus, before it can be definitely regarded as a generic feature. The fusion of the pads of the 3rd and 4th digits of the hind feet in these two genera—obviously a specialised feature—may be regarded as evidence of affinity between them; but the separation of these same pads in *Nandinia* and *Arctogalidia* is a case of the mutual inheritance of a primitive character, and cannot be considered as evidence of relationship.

* From the foregoing account of the hind feet of *Paradoxurus*, *Arctogalidia*, and *Nandinia* it will be seen that Mivart's description of the tarsus as "half-bald" in these genera is untrue, since by the term tarsus he meant the whole area between the plantar pad and the heel (P. Z. S. 1892, p. 206). He also included *Hemigaleus* (*Hemigalea*) in the category of genera with "half bald" tarsus, although his own figure of the hind foot of this genus (*op. cit.* p. 166) shows correctly that the greater part of the sole behind the plantar pad is covered with hair.

*Comparison between the Paradoxurine and Viverrine
types of feet.*

The feet of the Paradoxurine genera above described, and those of the Viverrine genera described in my previous paper (P. Z. S. 1915, pp. 132-140), may be briefly compared as follows:—

Viverrinae.—The pollical and hallucal elements of the plantar pads are either suppressed or small, and when present lie altogether behind the internal lateral lobe of the plantar pads so as to contribute nothing to the width of the latter. The carpal pads whether single or double are much shorter and narrower than the plantar pad, occupy only a small part of the underside of the carpo-metacarpal area, and are separated from the plantar pad by a tolerably long space, of which the median portion at least is covered with hair. The underside of the metatarsus is for the most part covered with hair; when the metatarsal pads persist, they are reduced to a small bilobed pad some distance away from the plantar pad (*Civettictis*), or to two narrow median ridges of integument in contact throughout the greater part of their length, slightly separated towards the heel and more strongly divergent inferiorly where they extend to right and left to meet the postero-lateral angles of the plantar pad, leaving a hairy space between (*Genetta*).

Paradoxurinae.—The pollical and hallucal elements of the plantar pads are large and comparable in size to the three remaining lobes of this pad individually, thus adding considerably to its width. The carpal pads are long and wide, occupy nearly the whole of the width of the underside of the carpo-metacarpal area, and conjointly equal or approximately equal the plantar pad in area; they are defined from it by a transverse groove which expands mesially into a depression, but this depression is never hairy. The metatarsal area is naked throughout the greater part of its length and width; when the metatarsal pads are retained they form two thick ridges of integument separated by a wide depressed area.

From this it is clear that the differences between the feet of these two groups are considerable. The differences in the case of the Viverrinae have arisen, as I have already pointed out (P. Z. S. 1915, p. 139), by the suppression or reduction in size of the pollical and hallucal elements of the plantar pads, by the reduction in size of the carpal pads, the growth of hair between them and the plantar pad, and by the suppression or reduction in size of the metatarsal pads and their replacement by normal hairy integument. In the case of *Genetta*, which of all the Viverrinae has the least specialised feet, it is clear that the two juxtaposed narrow ridges of skin extending along the middle line of the metatarsus are the homologues of the two thick ridges or pads, separated by a median depression, in *Paradoxurus* or *Arctogalidia*.

There is one other genus of Viverridæ which calls for attention here because its feet belong to the Paradoxurine type, though they differ in certain details from the feet of the genera to which that term is here restricted. This is the otter-like amphibious Civet *Cynogale*, which Gray first of all made the type of a special subfamily, afterwards raising it to family rank on characters held by Mivart to be trivial for that purpose. Mivart regarded *Cynogale* as an aberrant genus of his subfamily Viverrinæ, which embraced the Civets, Genets, Linsangs, Paradoxures, and others. The gland, however, was unknown both to Gray and Mivart. By this organ, as I have recently shown*, as well as by the structure of the muzzle and of the rhinarium, *Cynogale* differs considerably from the genera both of the Viverrine and Paradoxurine sections of Viverridæ, and cannot be included in either, as I define them, without unduly disturbing their homogeneity. In classifying this genus, therefore, I revert to Gray's original idea and regard it as the representative of a special subfamily, *Cynogalinæ*.

The Rhinarium and Vibrissæ of Paradoxurines.

In *Paradoxurus larvatus* the rhinarium is large and prominent. Viewed from the front its upper edge is markedly biconvex owing to the depth of the median groove and the curvature of the lateral angles. This groove extends uninterruptedly from a point close to the posterior border of the upper surface, over the anterior surface, where it is very deep, down to the edge of the lip in the middle line. The infranarial portion is large and extends laterally beyond the nostrils, where it curls up and narrowly borders them externally throughout their length on the upper side. Its inferior edge is horizontal with rounded angles. Just beneath the narial orifice in front, this infranarial portion is marked with a curved depression which runs downwards and inwards towards the middle line. This groove appears to correspond to the obliquely inclined infranarial edge of the rhinarium in *Canis* and *Felis*, the area external to the groove being covered with hair in those genera and other members of the families to which they belong.

Viewed from above, the convexity of the anterior edge is interrupted by a deep median angular notch—smaller in the young—and its posterior edge is concave. The narial slits converge inwards and backwards and are bordered externally by the narrow naked strip which is continuous in front with the superolateral angles of the large infranarial area. As a result of the backward and inward inclination of the narial slits, the upper field of the rhinarium is considerably wider in front than behind. Finally, it may be added, the hairy portion of the upper lip below the rhinarium is only about half the height of the anterior surface of the rhinarium itself.

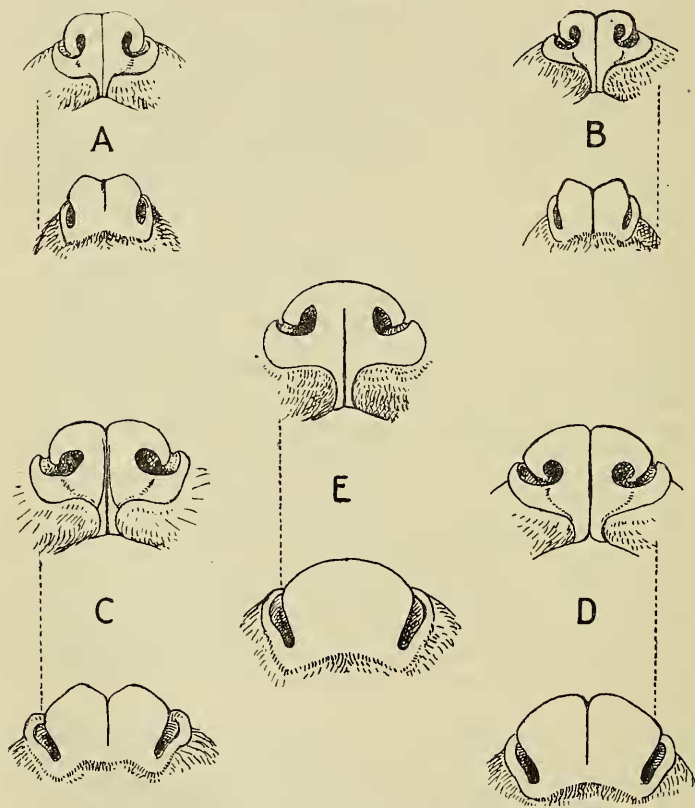
Comparing the rhinarium of *Paradoxurus* with those of the

* Ann. Mag. Nat. Hist. (8) xv. pp. 351-360, 1915.

Viverrinae described in my previous paper, it clearly resembles most closely that of *Viverra zibetha*, but its anterior and upper surfaces are much more deeply grooved, its superior angles on each side of the median notch are more prominent, and its upper surface is more markedly biconvex.

In *P. hermaphroditus* the rhinarium is like that of *P. larvatus* in all essential respects.

Text-figure 4.



Rhinarium, seen from the front and above, of A. *Nandinia*; B. *Arctogalidia*; C. *Paradoxurus larvatus*; D. *Arctictis*; E. *Civettictis*.

The rhinarium of *Arctogalidia* from the anterior aspect closely resembles that of *Paradoxurus*, but is narrower as compared with its height, and the lower edge of the infranarial portion slopes more obliquely upwards. Viewed from above, the median notch is wider and somewhat deeper, and the angles that define it are farther from the middle line and nearer the narial slits. These

slits, moreover, are subparallel and only slightly convergent posteriorly, so that the upper surface of the rhinarium is only a little narrower behind than in front.

In *Nandinia* the rhinarium, seen from the front, is a little narrower and higher than in *Arctogalidia*, its upper edge is less markedly biconvex, owing to the sulcus being shallower. The upper surface has a shallower anterior notch, and is a little longer as compared with its width than in *Arctogalidia* and is quite as wide behind as in front.

The rhinarium of *Arctictis* differs from those of the other Paradoxurine genera here described in one or two points. The median groove extends over the upper surface, but is sunk in a much shallower depression. Hence the superior margin of the anterior surface is not markedly biconvex, but is fairly evenly convex from side to side, with only a small and shallow median notch. Seen from above, this margin is similarly convex from side to side, with a small median notch. The infranarial portion in front is shallower and has a more evenly rounded inferior border, and, when seen from above, the narial slits converge posteriorly as in *Paradoxurus*.

In my description of the rhinaria of the Viverrine genera *Viverra*, *Civettictis*, etc., I said:—"It is impossible to affirm the existence of any absolute difference between the rhinaria of the Viverrinæ collectively and of the Paradoxurinæ." Confirmation of this is supplied by a study of this organ in the Paradoxurinæ; for, although the rhinarium of *Paradoxurus*, *Arctogalidia*, and *Nandinia* differs from that of the Viverrinæ in being very deeply sulcate above and in front, the rhinarium of *Arctictis*, a genus in most particulars the least Viverrine of all the Paradoxurinæ, is much less deeply and widely sulcate, its supero-anterior margin being evenly convex from side, to side with a quite small median notch. The convex curvature of this border recalls that of the rhinarium of the African Civet (*Civettictis*), although the median groove of the rhinarium is deeper both above and in front than in that genus. On the other hand, the rhinarium of the large Indian Civet (*Viverra zibetha*), with its upper surface biconvex, is more like the rhinarium of *Paradoxurus* than is the rhinarium of *Arctictis*. In the shape of this organ, therefore, the genera of Viverrinæ and Paradoxurinæ intergrade.

The facial vibrissæ may be briefly dismissed. The tufts are without exception normal in number, the mystacials in particular being long and rigid. Of the two genal tufts on each side, the inferior is situated in a line with the corner of the mouth and the superior a little higher up and posterior to it. The least developed is the interramal, but it is always present and not far behind the mandibular symphysis.

The Ear of Paradoxurines and Viverrines.

There appears to be no accepted terminology for the cartilaginous ridges which strengthen and support the pinna of the

ear in mammals, and by interlocking help to close the meatus when it is capable of being closed. Mivart described the pinna of the Common Cat ('The Cat,' pp. 295-296, 1881) and of the Genet (P. Z. S. 1892, p. 51, fig. 12), adopting for the several parts names originally applied to the human ear. An entirely different nomenclature was, however, proposed by Boas in 1912 ('Ohrknorpel und äusseres ohr der Säugetiere,' Kopenhagen). In the following account I have attempted to show the correspondence between these two systems and have, in the main, followed that of Mivart as being more familiar and more intelligible, without wishing thereby to cast any reflection upon the excellence of Boas' work.

In *Paradoxurus larvatus* the cartilaginous ridges, with their intervening fossæ, which strengthen the lower portion of the pinna round the auditory meatus, resemble those of the Cat and Genet in essential features. Two ridges run obliquely upwards and forwards in front of the inferior orifice of the meatus (*aditus inferior* of Boas). The outer of these, the *posteron 4* of Boas, carries a low elevation called the *tragus* by Mivart. The inner, the *anteron 6* of Boas, has a sinuous edge and runs higher up the front of the ear than the outer or tragus-bearing ridge. This inner ridge is called the post-tragus by Mivart in the case of the Cat, but in his figure of the Genet's ear it is marked tragus. Two ridges similarly run obliquely upwards and backwards from the inferior orifice of the meatus. The outer of these, the *posteron 6* of Boas, is produced inferiorly into a large angular process, the *antitragus* of Mivart, which fits into the lower part of the fossa between the two anterior ridges when the ear is closed. Above and within the outer ridge lies the inner of the two posterior ridges, which is much softer and less well developed than the others and shows a small swelling near its lower end. This ridge, an integumental non-cartilaginous structure, was not given a special name by Mivart, and was merely described as a "weiche Falte" by Boas. Nevertheless it appears to be a constant feature in the ears, at all events, of the Canidæ, Felidæ, and Viverridæ.

The four ridges above described, with their intervening fossæ, form the anterior and posterior walls of the deep and spacious fossa lying above the auditory meatus. This large fossa is defined above by a transverse cartilaginous ridge, the *plica principalis* of Boas and the *supratragus* of Mivart, the anterior end of which is overlapped by the inner of the two anterior ridges. Towards the middle of the ear it exhibits a marked swelling, and behind this the ridge gradually fades away towards the inner side of the inner of the two posterior ridges*.

* The cartilaginous thickening in the ear of the Carnivores, named *posteron 4* by Boas and *tragus* by Mivart, seems certainly to be the homologue of the "tragus" in the human ear. But the thickening named "antitragus" by Mivart and *posteron 6* by Boas is not, according to this latter author, the exact homologue of the human antitragus. This well-developed structure in man is part of another cartilaginous ridge, the *posteron 5* of Boas, which is at most feebly developed in the Carnivores, being merely represented by a weak ridge lying below and on the outer

The posterior margin of the ear, nearly in a line with the supratragus, is doubled to form a definite pocket, called the "pouch" by Mivart and the "Körbchen" or "Tasche" by Boas. For this I have proposed the name "*bursa*." The anterior flap of this is continuous above and below with the rim of the pinna, and its edge is deeply, widely, and angularly emarginate. The posterior flap, on the contrary, is semilunar with a continuously convex edge, the upper and lower ends of which are attached behind the rim of the pinna, as in the Genet and, I believe, all species of *Felis*.

Comparing the ear of *Paradoxurus larvatus* with that of the three genera of Viverrines—*Genetta*, *Viverricula*, and *Civettictis*—the following points may be noticed. In *Genetta dongolana* (Somaliland) the bursa is formed as in *P. larvatus*, except that the emargination of the anterior flap is nearly rectangular in the former and obtusely angular in the latter. In *Civettictis civetta* and *Viverricula malaccensis*, on the other hand, the anterior flap is less deeply and more widely emarginate and the convex edge of the posterior flap is continuous above and below with the rim of the pinna, instead of rising behind it. Also in these two the inner of the two anterior ridges carries a much larger process overhanging the anterior end of the supratragus (*antihelix* or *plica principalis*) than is to be seen in *Genetta dongolana* and *P. larvatus*.

In *Genetta dongolana* and *rubiginosa* the tragus is more markedly bilobed and the antitragus provided with a better developed external ridge, giving rise to the "double" condition described by Mivart in *G. tigrina*, than in *P. larvatus*. This external ridge is very well formed in *Viverricula*, but is not larger in *Civettictis* than in *Paradoxurus larvatus*.

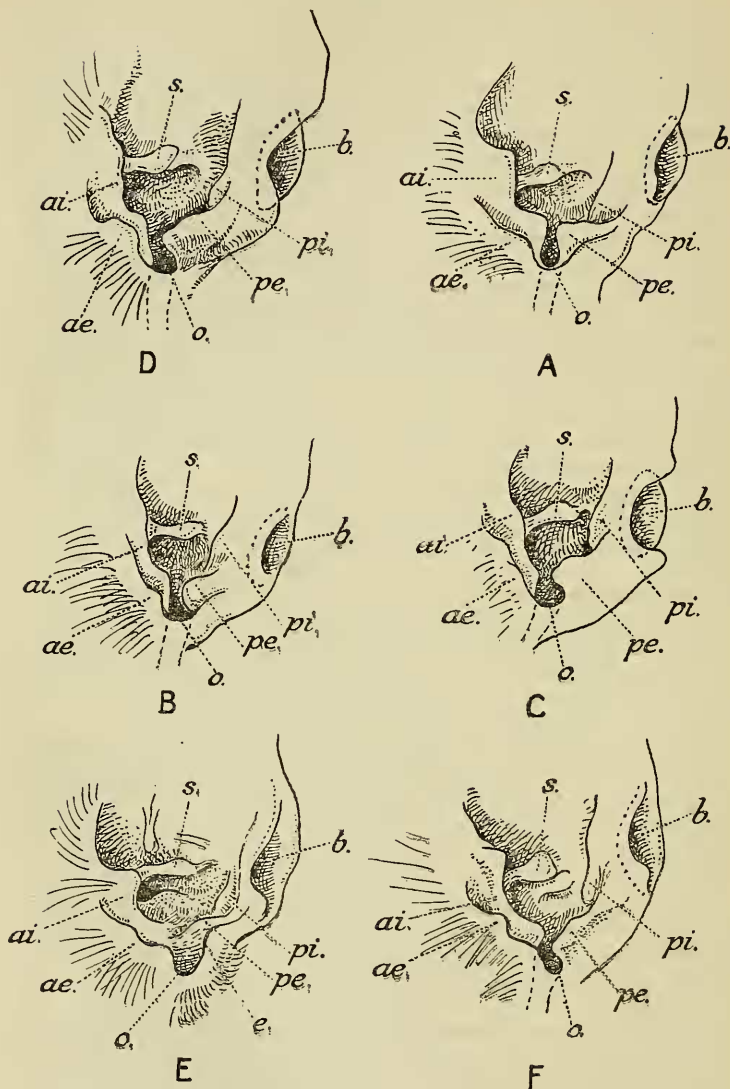
Apart, however, from the bursa, the ears of the four species are very much alike, and the recorded differences in the exact shape of the ridges must be tested in the case of other species of the genera before, in my opinion, it will be safe to attach systematic importance to them. They may be due merely to individual variation.

The ear of *Paradoxurus hermaphroditus* resembles that of *P. larvatus* except that the anterior flap of the bursa is more deeply and roundly emarginate and its angles, especially the inferior angle, are more produced.

I did not examine in a fresh state the ears of *Arctictis*. The only point of importance that could be made out on a dry skin was the presence of the bursa and its resemblance to that of *Paradoxurus larvatus*, in the origin of the upper end of the

side of the so-called antitragus. Mivart recorded the two ridges as a "double antitragus," a quite intelligible view. On the other hand, Mivart does not seem to have detected that the ridge he named the *post-tragus* (= *anteron* 6 of Boas) corresponds to the basal portion of the ascending helix in man, and that the *supra-tragus* (= *plica principalis* of Boas) is the homologue of part of the *antihelix* of human anatomists.

Text-figure 5.



Base of pinna of left ear of A. *Nandinia*; B. *Arctogalidia*; C. *Paradoxurus hermaphroditus*; D. *P. larvatus*; E. *Viverricula malaccensis*; F. *Civettictis civetta*.

b., bursa; o., inferior orifice of meatus; s., superior ridge (=supratragus of Mivart); ae., external of the two anterior ridges (=tragus of Mivart); ai., internal of the two anterior ridges (=post-tragus of Mivart); pe., external of the two posterior ridges (=antitragus of Mivart); pi., internal of the two posterior ridges; e., supplementary ridge outside pe. in *Viverricula*.

posterior flap from the back of the pinna and the continuity of the rim of the pinna with the upper end of the anterior flap. This flap, however, is much more widely and less deeply emarginate than in *P. larvatus*.

In *Arctogalidia* the cartilaginous ridges of the ear resemble in a general way those of *Paradoxurus larvatus*, but there is a distinct though small ridge on the outer side of the antitragus. The bursa, however, differs in one or two points. The margin of its anterior rim is not so deeply or abruptly excised, and its posterior rim is continuous above with the rim of the ear and does not arise behind it as in that genus. Hence the orifice of the bursa is more closed, and its posterior wall does not form a flap freely movable on its base of attachment. In other words, the bursa in *Arctogalidia* is more like that of *Viverricula malaccensis* and *Civettictis civetta* than of *Paradoxurus larvatus* and *Genetta*.

In *Nandinia binotata* the inner of the two anterior cartilaginous ridges differs from that of *Paradoxurus larvatus* and of *Arctogalidia* in the larger size and angular shape of its two processes. As in *Arctogalidia*, the antitragus carries an external ridge. The bursa resembles that of *Paradoxurus*, *Arctictis*, and *Genetta* in the origin of its posterior flap from the back of the pinna, but the angular excision of its anterior flap is shallower than in *Paradoxurus*, but deeper than in *Arctictis*.

From the foregoing account it will, I think, be clear that it is impossible to make use of the ears in differentiating the Viverrinæ from the Paradoxurinæ. Nevertheless, within the limits of these two subfamilies the structure of these organs, and especially of the bursa, will probably be found useful for distinguishing genera.

I am quite unable to surmise what meaning is to be attached to the variation in the structure of the bursa, by which the genera above discussed may be grouped as follows:—

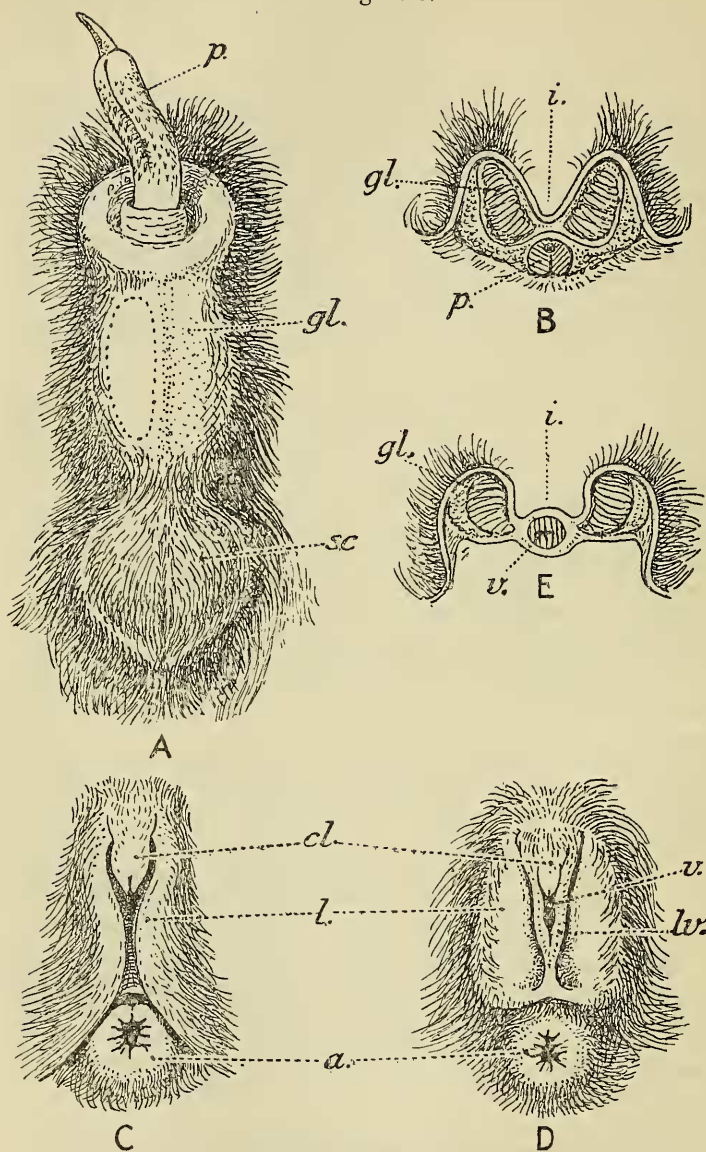
- a. Posterior flap of bursa arising above behind the rim of the pinna *Genetta*, *Paradoxurus*, *Arctictis*, *Nandinia*.
- b. Posterior flap of bursa continuous above with the rim of the pinna *Viverricula*, *Civettictis*, *Arctogalidia*.

Since the condition of the bursa found in Canidæ, Felidæ, and some of the Arctoid Carnivora is the same as that described under heading *a*, this condition is probably the primitive one. Probably, also, the condition described under heading *b* is the beginning of the suppression of the bursa, a process which is completed in some Æluroid and some Arctoid Carnivores.

The Perfume-gland and External Genitalia of Paradoxurus.

One of the earliest descriptions of the gland and genitalia of *Paradoxurus* was published under the name *Platychista pallasii* (= *Paradoxurus hermaphroditus*) by Otto (Nova Acta Acad. Leop.-Car. xvii. p. 1089, pl. lxxiii, 1835). Except in the structure of

Text-figure 6.

*Paradoxurus larvatus.*

- A. Gland and external genitalia of male. *gl.*, glandular area with the position of the right gland dotted in, the median depression not represented; *p.*, glans penis; *sc.*, scrotum.

(Continued at foot of next page.)

the penis and its precise relations to the gland, the figure accompanying the description agrees with my own observations.

A year later Hodgson (Asiatic Res. xix. p. 77, 1836) described the perfume-glands of three species referred to *Paradoxurus*, namely, *hirsutus*, *nipalensis*, and *lanigerus*. According to Blanford the name *hirsutus* was applied to the two species now known as *niger* and *hermaphroditus*; *nipalensis* is a synonym of *grayi*, but the species named *lanigerus* can only be assigned to the genus with hesitation. By the system of classification now in use, *niger* and *hermaphroditus* belong to the genus *Paradoxurus* and *grayi* to the genus *Paguma*; and I do not doubt that *lanigerus* is also a *Paguma*.

Hodgson detected no difference between the glands of the species he examined; and although he examined both males and females, his description suggests that the glands in the two sexes are alike in their relations to the vulva and penis. This, however, is not the case, as will be explained, since the penis is situated at the anterior end of the naked glandular area and the vulva lies near its centre.

Mivart's description of the scent-glands as lying "beneath the surface of a valve-like antero-posteriorly directed cutaneous inflection, more or less naked, and situated between the penis and testes in the male and analogously in the female," conveys very little idea of their structure (P. Z. S. 1882, p. 163).

Turner's very brief description of the gland of *P. niger* (= *typus*) as an oval, flat, naked space at the base of the prepuce, although wanting in preciseness as to the situation of the gland, is accurate and intelligible (P. Z. S. 1849, p. 25).

The main portion of the gland in the male consists of a pair of thickened ridges of skin or labia extending between the scrotum and the penis. These labia form the side-walls of a longitudinal fossa which is everywhere perfectly smooth; but the margin and outer surfaces of the labia are covered with long hair. The paired glandular thickening, which makes these labia, does not extend so far forwards as the penis, but a rim of thickened skin, naked internally, hairy externally, passes forwards in front of them and encircles the base of the penis like a collar. The narrow space between the collar and the penis is highly glandular,

Description of text-figure 6, *continued*.

- B. Transverse section of the glandular area of the same; *gl.*, gland of right side; *i.*, glandular space bordered by the two labia; *p.*, penis.
- C. Gland and external genitalia of female. *cl.*, clitoris; *l.*, left labium of gland folded over glandular area; *a.*, anus.
- D. Same as fig. C, with labia of gland (*l.*) pulled apart to show vulva (*v.*) and narrow labia of vulva (*lv.*). *a.*, anus; *cl.*, clitoris.
- E. Transverse section of same behind vulva. *gl.*, gland; *i.*, glandular space bounded by the two labia; *v.*, vagina.

the secretion having a repulsive odour. The secretion of the paired gland has a "mousy" smell and is poured over the naked skin of the fossa between the two labia. These labia are capable of being widely separated so that the glandular area may be flattened, but they are not closely applied and separated merely by a narrow *rima*, like the labia of the homologous gland in *Viverra* and *Genetta**. The glans of the *penis* is long, flexible, subcylindrical, weakly grooved below, and beset with recurved horny papillae. It ends in a styliiform process.

The arrangement in the female is tolerably similar. The labia of the gland arise in front on each side of the clitoris and pass backwards to the anal area. They are naked on the inner side, but hairy externally as in the male. Anteriorly they lie outside the hairy labia of the vulva, which lies just behind the clitoris; and the labia of the vulva unite posteriorly and form a low ridge of naked integument which runs along the bottom of the space between the labia of the gland and spreads to right and left, forming a short transverse ridge in front of the anal area. The labia of the gland can be folded over the vulva and the naked glandular space behind the clitoris, exactly as in the male the corresponding labia can be folded over the glandular space behind the penis; but in the female these labia are not closely applied as they are in *Genetta* and *Viverra*.

The anal area in both sexes is tolerably large and naked as in *Genetta* and *Civettictis*, but the repulsive secretion of the anal glands is not retained by an annular ring of skin as in *Viverra zibetha*.

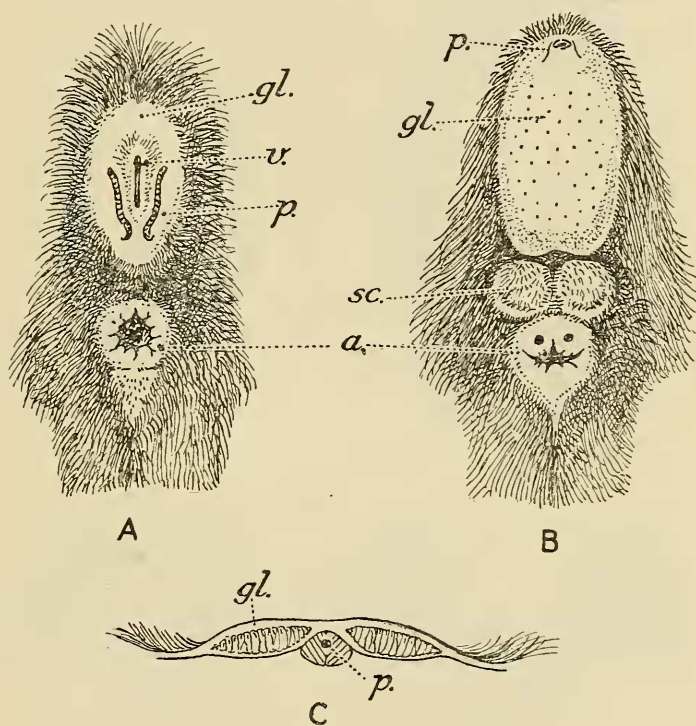
In male examples of *Paradoxurus niger* and *P. hermaphroditus* the glandular area closely resembles in its general features that of *P. larvatus* in consisting of a naked, elongated, tongue-shaped area of whitish glandular integument extending from the scrotum behind round the prepuce in front. But there is no thickened collar of skin round the penis and the labia of the gland are much less pronounced, so that when the thighs are separated the glandular surface forms no definite median fossa but is almost flat from side to side. When, however, the inner surfaces of the thighs are in their normal position and juxtaposed, the right and left halves of the glandular surface are brought into contact. The degree of development of these labia may prove to be a generic difference between *Paguma* and *Paradoxurus*. At all events, the conditions described hold good in the case of two species of each of the genera as recognised by Gray. The penis of *Paradoxurus niger*, judging from Turner's description (P. Z. S. 1849, p. 25), resembles that of *P. larvatus*, and the same applies to the penis of *P. hermaphroditus* that I examined.

In a half-grown female of *P. hermaphroditus* the glandular area consists of a nearly flat area of naked skin, without distinct labia. The vulva lies near its centre, and on each side of the

* The gland in a living example of *P. leucomystax* resembles apparently that of *P. larvatus*.

vulva there extends backwards a shallow groove beset with a row of coarse pores. The anterior end of each groove reaches as far forwards as the corresponding end of the vulva, but the posterior end reaches considerably farther back, nearly to the hinder end of the area of naked skin. The low ridges between these posteriorly converging grooves and the vulva are scantily hairy, and constitute the labia of the latter orifice.

Text-figure 7.

*Paradoxurus hermaphroditus.*

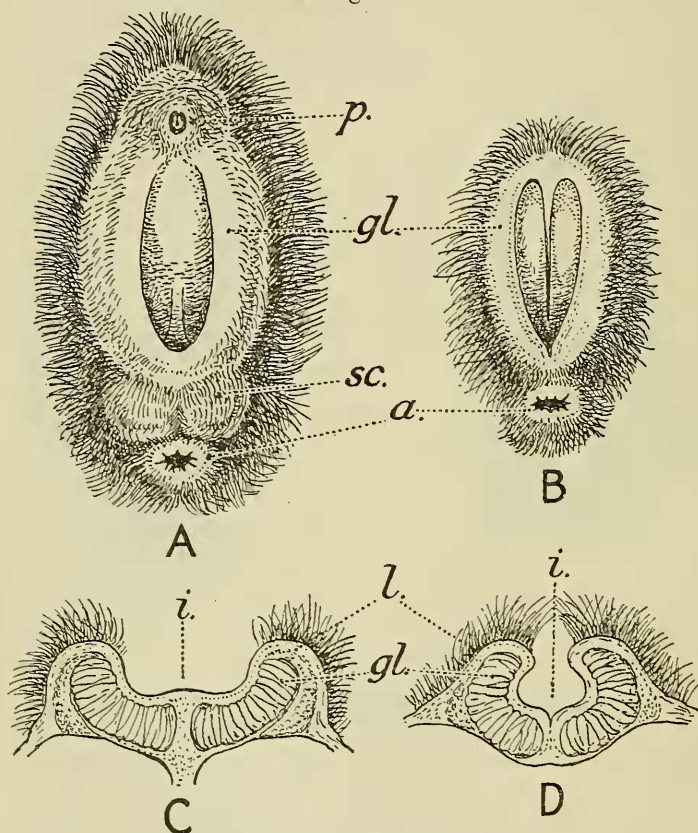
- A. Gland and external genitalia of half-grown female. *gl.*, anterior end of glandular area; *v.*, vulva, surrounded by short hairs; *p.*, row of secreting pores; *a.*, anus.
- B. The same of adult male. *gl.*, glandular area flattened; *p.*, prepuce at its anterior end; *sc.*, scrotum; *a.*, anus, with orifices of anal glands.
- C. Transverse section of glandular area of male. *gl.*, right portion of gland; *p.*, penis.

This gland differs from that of the female *P. larvatus* in the absence of distinct labia, as in the case of the males of the two species.

The Perfume-gland and External Genitalia of Arctictis.

The gland of the male was first described by Cantor (J. A. S. Bengal, 1846, p. 192), and subsequently by Garrod (P. Z. S. 1873, p. 200). It resembles that of *Paradoxurus larvatus* in consisting

Text-figure 8.

*Arctictis binturong.*

- A. Gland and external genitalia of male. *gl.*, glandular area showing labia and central depression; *p.*, prepuce. *sc.*, scrotum; *a.*, anus.
 B. Gland of the female (vulva omitted); lettering as in A.
 C & D. Transverse sections of the same with the labia of the gland partially distended and nearly in contact. *gl.*, gland of one side; *i.*, glandular space between the labia (*l.*).

of a pair of upstanding labia, hairy externally, smooth internally, extending from the scrotum up to the penis, and separated by

a naked fossa which becomes gradually shallower towards the penis. There is no definite collar of skin round the prepuce but integument, resembling that of the free edge of the labia in being scantily covered with yellow hair, encircles that organ. The posterior end of the fossa is partially divided by a low membranous partition when the labia are not widely divaricated.

The penis, which I omitted to examine, was described by Garrod as follows: "The glans penis is conical and pointed, $\frac{3}{4}$ inch long, and presents round its base several small, dark brown, hard flattened papillæ about $\frac{1}{12}$ inch long." From this it may be inferred that the glans is shorter than in *Paradoxurus*, has no styliform termination, and is further distinguished by the restriction of the papillæ to its base, their smaller number and flattened, unspine-like shape.

The gland of the female does not appear to have been described. It is very like that of the male, consisting of a small longitudinal fossa, with an upstanding labium, hairy without and naked within, on each side of it. As in the male and in *Paradoxurus*, these labia, which converge anteriorly and posteriorly, are capable of being widely divaricated, but they are not tightly juxtaposed as is the case with the homologous labia of *Viverricula*, *Genetta*, etc. When only partially divaricated, the floor of the fossa rises into a low median ridge of skin. The vulva is situated in front of the glandular area, not near its centre as in *Paradoxurus*. The glandular area is thus wholly perineal as in the Viverrines.

The Perfume-gland and External Genitalia of Arctogalidia.

The gland in this genus does not appear to have been described. Temminck and S. Müller, as Mivart stated, are silent about it. Hence Mivart presumed the gland to be as in *Paradoxurus* (P. Z. S. 1882, p. 165). On the other hand Blanford (Mamm. Brit. India, p. 115, 1888) said: "there is no bald space in front of the scrotum or around the genital orifice; hence it is probable that the prescrotal glands, if they exist, are ill developed." What material Blanford had whereon to base this opinion does not appear; but the concluding sentence of the quotation suggests that the result of his examination, presumably of dried skins, was unsatisfactory. At all events his remarks do not justify Lydekker's statement that "there is no glandular tract in front of the scrotum" (Lloyd's Nat. Hist. : Cats. etc. p. 230, 1896).

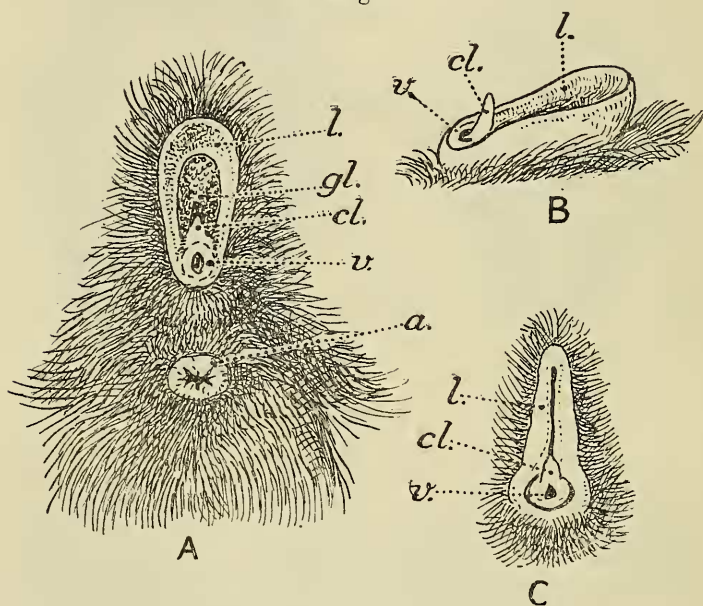
I can say nothing about the gland in the male, but a female example identified as *A. leucotis*, from Sarawak, has a distinct though small naked glandular tract in front of the vulva; or rather, since the naked integument narrowly encircles the vulva behind, that orifice, preceded by a well-developed clitoris, may be described as situated at the posterior end of the glandular area. The area itself is antero-posteriorly elongated and is surrounded

laterally and in front by an upstanding flap of quite naked skin capable of being flattened out externally and anteriorly, or folded over towards the middle line to form a pair of elongated labia in contact throughout their length in front of the clitoris and vulva.

The part of this naked area which appears to be specially active lies just in front of the clitoris.

Behind the vulva there is a moderately long hairy, non-glandular, perineal tract, so that the anus, situated in the centre of a small, normal naked space, is remote from the glandular area.

Text-figure 9.



Arctogalidia.

- A. Gland and external genitalia of female. *gl.*, secreting area of gland; *l.*, partially distended upstanding labia surrounding it. *cl.*, clitoris; *v.*, vulva; *a.*, anus.
 B. Lateral view of the same; lettering as in A.
 C. Glandular area showing the labia folded in front of the clitoris; lettering as in A and B.

Since glands are present in both sexes of the genera of Paradoxurine Viverrids described in this paper, and are better developed in the males than in the females, it can hardly be doubted that the male of *Arctogalidia* is also provided with a gland; but it appears to me to be impossible to foretell whether the gland of the male will prove to be in front of the penis or behind it. Perhaps the balance of evidence is in favour of its

being prepenial, instead of prescrotal as in *Paradoxurus* and others*.

However that may be, the gland of the female *Arctogalidia* differs from that of *Paradoxurus* in several respects. In *Arctogalidia* the principal secreting area is the depression in front of the clitoris, encircled by an upstanding flap of thin skin naked without and within and apparently not specially glandular. The right and left portions of this flap form two labia confluent in front and capable of being folded over the glandular depression, thus meeting *in front* of the clitoris and vulva. Between the vulva and the anus there is a tolerably long hairy perineal area. In the female *Paradoxurus* the labia are thick, glandular, and hairy externally. They are not confluent in front but arise separately at the sides of the clitoris, pass backwards on each side of the vulva and extend some distance behind it, almost reaching the anal area, being separated therefrom by a very short hairy non-glandular area. When folded over they meet in the middle line *behind* the clitoris.

The Perfume-gland and External Genitalia of Nandinia.

The gland of the male was described by Flower (P. Z. S. 1872, p. 684) as follows:—" *Nandinia* resembles many of its allies in possessing a ... cutaneous scent-gland in the form of a longitudinal median depression an inch in length, with tumid naked margins and looking very like a vulva, situated in the pubic region immediately in front of the short, conical retroverted hairy prepuce." This description is perfectly correct, but it unfortunately suggests similarity in position between this gland and that of the typical Paradoxurines.

Ten years later Mivart (P. Z. S. 1882, p. 170, note) made a similar mistake when he described the gland as "a bald patch, no doubt glandular, in the situation of the prescrotal glandular structure of *Genetta*." It is quite true that the gland in *Nandinia* is prescrotal, but it does not lie between the scrotum and the penis as in *Genetta*, but in front of the penis as Flower stated.

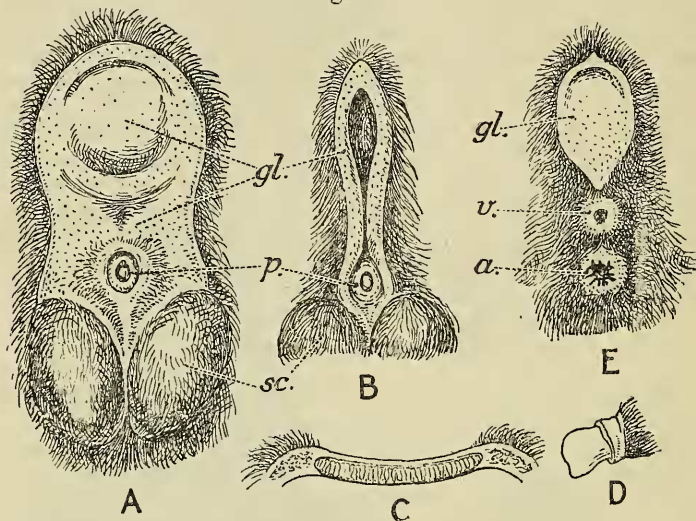
In 1900 Miss Carlsson (Zool. Jahrb. Syst. xiii. pp. 509-528) figured and described the gland of the female as a narrow area of naked skin situated in front of the vulva and ending anteriorly in a distinct pouch. This had been previously detected by Noack, who regarded the pouch as the functional homologue of the marsupial pouch (Zool. Garten, Frankfurt, xxvii. p. 79, 1886).

In a half-grown female *Nandinia* I found the glandular area exactly as described by Miss Carlsson, except that it was separated from the vulva by a narrow area covered with hair and had only an indistinct pouch at its anterior end. It consisted of an elliptical patch of pale naked skin, with the anterior rim slightly

* If this proves to be so, a good case might be made out for severing *Nandinia* and *Arctogalidia* from the Paradoxurinae as a separate subfamily Nandiniinae.

raised. Probably as age advanced, the pouch would have been developed and possibly the area would have extended backwards to join the naked skin surrounding the vulva. The skin overlying the gland was thin, and the secretion was brown in colour and strong in odour.

Text-figure 10.

*Nandinia binotata.*

- A. Gland and external genitalia of adult male. *gl.*, glandular area flattened; *p.*, prepuce surrounded by short hair; *sc.*, scrotum concealing anus.
- B. The same with labia of gland folded in front of prepuce; lettering as in A.
- C. Transverse section of gland in front of penis.
- D. Glans penis, its dorsal side uppermost.
- E. Gland and external genitalia of young female. *gl.*, glandular area; *v.*, vulva; *a.*, anus.

In the adult male the naked glandular area extends from the scrotum a long way in advance of the penis, which is situated near its posterior end, only a little in advance of the scrotum. Close to the penis on each side there are some hairs, sometimes forming a definite crest, sometimes more numerous and less regularly arranged. Sometimes there are also a few hairs right in front of that organ, but for the rest of the area it is quite smooth. The anterior half of the area expands and forms, when the gland is flattened out by the separation of the thighs, a shallow subcircular depression with tumid margins; but when the thighs are juxtaposed the right and left halves of the area approach, or nearly meet, across the middle line, being separated by a moderately deep fossa the width of which depends upon the

degree of approximation of the right and left halves of the area. When its margins meet in front of the penis, these present the appearance, described by Flower, of two naked ridges of skin running forwards from the penis.

In longitudinal and transverse sections the gland is seen to consist of a comparatively thin layer of dermal cells, of tolerably uniform thickness transversely but gradually increasing in thickness from behind forwards. The secreting cells are not differentiated into a right and left thickening as in *Paradoxurus*, *Arctictis*, and the Viverrines. The prepuce is hairy, and the glans of the penis is quite short, a little expanded and rounded distally, and without spicules.

General Conclusions with regard to the Perfume-glands.

From the account here given it is clear that the gland in the Paradoxurines varies greatly in position in the genera discussed; but it is interesting to note the gradation in the situation it assumes, especially in the female. In *Arctictis* it is entirely perineal, lying between the anus and the vulva as in *Genetta*, *Viverra*, etc., and in *Hemigalus* and *Cynogale*, although differing structurally from the gland in those genera. In *Paradoxurus* the glandular area passes anteriorly in front of the perineum, so that the vulva lies near its centre. Nevertheless, the labia of the gland, as in *Arctictis*, fold over behind the vulva and clitoris. In *Arctogalidia* the external genital organs are situated quite at its posterior extremity, the secreting area being in front of the clitoris and the labia also folding anteriorly to it. In *Nandinia* the gland is altogether in front of the vulva and disconnected from it. Thus *Nandinia* and *Arctictis* stand at the two extremes.

In the males the differences between *Arctictis* and *Paradoxurus* on the one hand, and *Nandinia* on the other, are equally well marked, but the link in the chain of gradation is wanting, possibly owing to our ignorance of the gland in this sex of *Arctogalidia*.

Another point to consider is which of the two conditions presented respectively by *Arctictis* or *Paradoxurus* and *Nandinia* is the more primitive. I incline to the opinion that the latter is the derivative type; and for this reason—the position of the prepuce considerably in advance of the scrotum is the condition occurring in the Canidæ, Procyonidæ, and Ursidæ, which are the most generalised, on the whole, of existing Carnivores. It also obtains in the Æluroid *Cryptoprocta*. In the Pinnipedia, too, the prepuce is situated a long way in advance of the anus, close to which the scrotum was probably placed before its suppression. On the other hand, the position of the penis just in front of the scrotum is a character in which *Nandinia* resembles the Felidæ, which are regarded as the most specialised of all the Carnivora.

The opinion above expressed can only be tentatively held,
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however, because the prepuce is close to the scrotum in the Mongooses.

The main features of the glands and external genitalia may be systematically summarised as follows :—

Males*.

- | | |
|--|---------------------|
| a. Glands paired, situated behind the prepuce, which lies far in advance of the scrotum at the anterior end of the naked glandular tract; hence the labia of the gland when juxtaposed meet behind the prepuce. Glans penis long or moderately long, and spicular. | |
| a'. Glans penis subcylindrical, long, richly spicular, and terminated by a styliform process | <i>Paradoxurus.</i> |
| b'. Glans penis conical, shorter, spicular at base, and without styliform terminal process | <i>Arctictis.</i> |
| b. Glands unpaired, situated in front of the prepuce which is close to the scrotum; hence the labia of the gland when juxtaposed meet in front of the prepuce; glans penis quite short and unarmed | <i>Nandinia.</i> |

Females.

- | | |
|--|----------------------|
| a. Glands paired, behind and sometimes partially alongside the vulva; labia of the glands when juxtaposed meeting behind the clitoris and vulva. | |
| a'. Vulva in front of the large naked glandular area | <i>Arctictis.</i> |
| b'. Vulva near the middle of the naked glandular area, the secretory area extending behind and alongside the vulva ... | <i>Paradoxurus.</i> |
| b. Glands unpaired, secreting area altogether in front of the vulva; labia of the glandular area, when juxtaposed, meeting in front of the vulva. | |
| a ² . Vulva situated at the posterior end of the naked glandular tract which is bounded laterally and in front by up-standing labia | <i>Arctogalidia.</i> |
| b ² . Vulva separated from the naked glandular tract which has a pouch-like depression at its anterior end | <i>Nandinia.</i> |

Considered collectively the glands of these genera differ from those of the Viverrinæ in the following particulars :—In the Viverrines the labia of the glands are hairy without and within and form a pair of tumid masses usually closely juxtaposed or as in *Viverra zibetha*, where they are divergent behind, confluent in front behind the prepuce. In no case does the glandular area extend in front of the prepuce or of the vulva, nor does it ever form a flattened naked area covered all over with secretory orifices. In the Paradoxurine genera, on the contrary, the labia, when present as upstanding ridges, are naked within, like the floor of the fossa between them. They are not closely applied and can be so widely divaricated in both sexes that the secreting surface, studded all over with pores, forms a flat or nearly flat area.

* The glands of this sex in *Arctogalidia* are unknown.